

## REPTILIA: SQUAMATA: VIPERIDAE

## CROTALUS TORTUGENSIS

## Catalogue of American Amphibians and Reptiles.

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***Crotalus tortugensis* Van Denburgh and Slevin**  
Tortuga Island Rattlesnake

*Crotalus tortugensis* Van Denburgh and Slevin 1921:398. Type locality, "Tortuga Island, Gulf of California, [Baja California Sur] Mexico." Holotype, California Academy of Sciences (CAS) 50515, adult male, collected by J.R. Slevin, 22 June 1921 (examined by CLS).

*Crotalus atrox sonoraensis*: Amaral 1929:85.

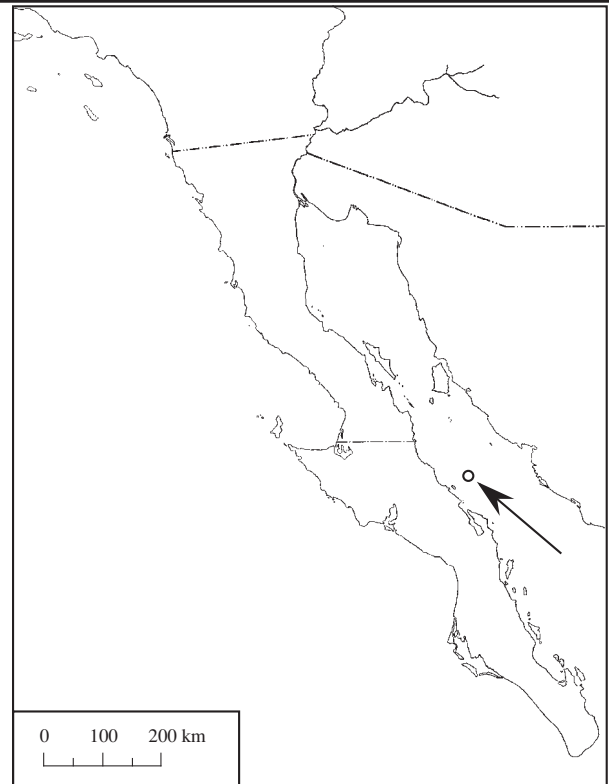
*Crotalus atrox tortugensis*: Stejneger and Barbour 1933:133.

• **CONTENT.** The species is monotypic.

• **DEFINITION.** *Crotalus tortugensis* is a medium sized rattlesnake, smaller than its nearest relative, *C. atrox* (Murphy et al. 2002), with large males reaching one meter in total length. The largest specimen on record is 1058 mm total length (Klauber 1972). This species is heavy-bodied and stout, with a triangular head. The head length is approximately 3.8% of the total body length for adult males, compared to 4.5% for males of *C. atrox* (Spencer 2003), a characteristic that may indicate dwarfing (Campbell and Lamar 1989). The scutellation is as follows (ranges and means are based on measurements of 39 snakes by CLS; all head scale counts are for right side only): midbody scale rows, 23–27 (25.8); ventrals (following the method of Dowling 1951), 174–194 (183.4); preentrals, 2–6 (3.7); subcaudals, 16–25 (21.4); canthals, 2; intercanthals, 1–3 (1.8); scales before supraoculars, 9–21 (15); minimum scale rows between supraoculars, 4–5 (4.4); nasals, 2; internasals, 0–1 (0.8); loreals, 1–2 (1.0); preoculars, 2; suboculars, 3–4 (3.2); interocularials, 2–3 (2.3); location of postocular pale stripe (number of scales anterior to the rictus, 0 is at rictus), 0–3 (1.5); interrials, 25–32 (28.8); prefoveals, 4–9 (5.8); postfoveals, 2–4 (3.7); lacunals, 2; supralabials, 14–17 (15.3); infralabials, 14–19 (16.6); percent divided first infralabials, 18.0%; gulars, 5–8 (6.5); intergenials, 0–1 (0.18); percent prenasal contact with first supralabial, 97%; percent postnasal contact with preocular, 5.1%; number of body blotches, 29–41 (35.4); number of tail rings, 3–6 (4.6); and number of rattle fringe scales, 10–18 (12.7).

Adult male body size ranges from 592–1058 mm and adult female body size from 651–881 mm (Klauber 1972; this study). Other mensural characters are as follows (range of measurements noted in mm; methods follow Spencer 2003; measurements of the right side of the head are listed where applicable) for adults males: ratio of rostral height to rostral length, 0.88–1.34 (1.09); head length, 26.10–38.10 (33.60); head height, 8.05–17.65 (11.25); head width, 18.50–28.50 (23.60); and tail length, 41–77 (61). Other mensural characters for adult females are as follows (see previous notes): ratio of rostral height to rostral length, 0.85–1.43 (1.08); head length, 26.60–40.65 (32.36); head height, 6.00–13.60 (10.78); head width, 17.60–25.10 (22.14); and tail length, 37–60 (48).

Dorsal ground color is gray to dark brown, often with a purplish or pinkish tinge. The head has scattered black flecks. Body blotches are purplish-brown to dark brown, and are diamond or hexagonal-shaped with black mottling. The margins of blotches on the anterior two-thirds to three-fourths of the body are white or buff along the dorsal midline; these light margins are absent along the lateral edges of the blotches (Campbell and Lamar 1989). The body is punctuated with small black spots, creating a dusty look. Pale colored pre- and postocular stripes are present.



**MAP.** The circle indicated by an arrow points to Isla Tortuga, the type locality and entire known range of *Crotalus tortugensis*.



**FIGURE.** *Crotalus tortugensis* from Isla Tortuga, Baja California Sur, México (photograph by L.L. Grismer).

The pale postocular stripes end before the rictus of the mouth. A darker stripe is present posterior to the pale postocular stripe. Similar to *C. atrox*, the tail has a distinctive and contrasting color pattern of black and ash-white alternating stripes. The black caudal rings are as wide or wider than the white rings and the black rings are sometimes not continuous.

• **DIAGNOSIS.** *Crotalus tortugensis* is most similar to *C. atrox*, with differences in the dorsal blotches (diamonds) being the most noticeable divergence. The blotches are less distinct than in *C. atrox*. In *C. tortugensis*, the margins of the blotches are much darker than the central portion and usually "include on each side [of the blotch] a group of lighter scales as pale as the general dorsal ground color" (Van Denburgh and Slevin 1921). These

paler colored scales may be found throughout the blotches and may connect across the dorsum. Klauber (1930) stated that the "light borders of the diamonds characteristic of *atrox* are absent except along the middorsal line," and Grismer (2002) noted that the white scales of the anterior borders of the diamonds are often reduced or absent in *C. tortugensis*, and that the diamonds fade posteriorly.

A unique trait noted by several authors is the absence of an upper (second) loreal in *C. tortugensis* (Klauber 1972, Campbell and Lamar 1989, Grismer 2002). Of 39 *C. tortugensis* examined in this study (CLS), 38 specimens had a single loreal, with only one snake (SDSNH 27082) having two loreals on both right and left sides of head. The postnasal and preocular scales are rarely in contact (3–5%; Klauber 1930; this study). In *C. atrox*, the opposite trend occurs with 94–95% of snakes having the postnasal in contact with the preocular scale or contact prevented by a loreal, usually the upper loreal (Klauber 1930, Spencer 2003).

An additional scale character that differentiates *C. tortugensis* from *C. atrox* is the intergenials. In *C. tortugensis*, 25.6% of the snakes examined (10 of 39) possessed at least one intergenial scale. Four of 39 (10.3%) snakes had two intergenials, one on both the left and right sides of the jaw. This scutellation was not observed in 922 *C. atrox* examined (Spencer 2003).

Brattstrom (1964) noted an osteological difference between *C. tortugensis* and *C. atrox*, namely that *C. tortugensis* had a squamosal relatively shorter than does *C. atrox*. This is one of the few osteological characters in which *C. tortugensis* falls outside the range of measurements of *C. atrox* (Brattstrom 1964).

*Crotalus tortugensis* can be differentiated from *C. ruber* by the percent of division between the first infralabials. *Crotalus ruber* has a higher frequency of divided first infralabials (90–100%; Klauber 1930) compared to only 11–18% of individuals possessing the same character in *C. tortugensis* (Klauber 1930; this study). *Crotalus tortugensis* may be differentiated from *C. ruber exsul* by possessing fewer numbers of intergenials. Klauber (1930) found that 92% of *C. r. exsul* had intergenials, whereas only 15–26% of *C. tortugensis* have intergenials (Klauber 1930; this study). *Crotalus tortugensis* can be differentiated from all remaining *Crotalus* by two characters: the postocular stripe ending at or before the rictus and the tail having alternating black and white rings that are in marked contrast to the body color.

• **DESCRIPTIONS.** The original description was published by Van Denburgh and Slevin (1921). Additional descriptions appeared in Van Denburgh (1922), Gloyd (1940, 1978), Campbell and Lamar (1989, 2004), Mattison (1996), Rubio (1998), McPeak (2000), and Grismer (2002).

• **ILLUSTRATIONS.** Black and white photographs of *Crotalus tortugensis* were published in Gloyd (1940), Klauber (1956, 1972), Harris and Simmons (1977, 1978), and Glenn and Straight (1982). Color photographs were published in Campbell and Lamar (1989, 2004), Mattison (1996), Rubio (1998), McPeak (2000), and Grismer (2002). A black and white photograph published by Harris and Simmons (1977) and a color photograph in Grismer (2002) depict the habitat on Isla Tortuga.

• **DISTRIBUTION.** *Crotalus tortugensis* is endemic to Isla Tortuga, Baja California Sur, México.

• **FOSSIL RECORD.** None.

• **PERTINENT LITERATURE.** Murphy (1976, 1982, 1983a, b), Grismer (1994a,b), Mattison (1996), and Murphy and Aguirre León (2002) discussed the origin and evolution of *C. tortugensis* in Baja California. Phylogenetic relationships were discussed

by Cliff (1954a,b), Klauber (1956, 1963, 1972), Radcliffe and Maslin (1975), Campbell and Lamar (1989, 2004), and Murphy et al. (1989, 2002). Case (1983, 2002) commented on the relationship of body size to prey size and availability.

Additional aspects of biology are as follows: **evolution** (Brattstrom 1964, Murphy et al. 2002), **evolution of insular body size** (Case 1978), **taxonomy** (Schmidt 1922; Werner 1923; Harris and Smith 1979; Underwood 1979; Mattison 1996; Rubio 1998; Grismer 1999a, 2002; Campbell and Lamar 2004), **morphology** (Klauber 1936a,b, 1937, 1938, 1939, 1940, 1943; Amaral 1944; Cliff 1954a,b; Altman and Ditmer 1962; Stille 1987; Campbell and Lamar 1989, 2004), **venom** (Klauber 1956, 1972; Bücherl and Buckley 1971; Brown 1973; Gans 1978; Russell 1979, 1980; Glenn and Straight 1982, 1985; Mattison 1996), **genetics** (Stewart and Morafka 1989, Stewart et al. 1990), **physiology** (Skoczylas 1978), **courtship and mating behavior** (Armstrong and Murphy 1979), **natural history** (McPeak 2000, Grismer 2002), **reproduction** (Mattison 1988, Grismer 2002), **diet** (Van Denburgh 1922; Klauber 1956, 1972), **parasites** (Riley and Self 1979, Rego 1980/1981), **conservation** (Tryon 1986, Flores Villela and Gerez Fernandez 1988), **longevity** (Perkins 1948, 1950, 1951, 1952, 1953, 1954, 1955; Shaw 1957; Bowler 1977; Slavens 1978–2000; Snider and Bowler 1992), and **capitive management** (Perkins 1948, 1950, 1951, 1952, 1953, 1954, 1955; Shaw 1957; Murphy and Armstrong 1978; Slavens 1978–2000; Anonymous 1979; Mattison 1988; Snider and Bowler 1992).

The following authors mentioned its occurrence on Isla Tortuga, Baja California: Schmidt (1922), Ditmars (1930, 1931), Klauber (1930, 1956, 1971, 1972, 1982), Martín del Campo (1935), Mayr (1942), Savage (1952), Cliff (1954a,b), Wright and Wright (1957), Lindsay (1962, 1964), Carlquist (1965), Hoge (1966), Soule and Sloan (1966), Russell (1969), Hoge and Romano (1971), Caras (1974), Ruth (1974), Harris and Simmons (1977, 1978), Armstrong and Murphy (1979), Underwood (1979), Kissner (1980), Hoge and Romano-Hoge (1981), Kilmon (1981), Russell (1983), McCoy (1984), Murphy and Ottley (1984), Phelps (1984), Mattison (1986, 1996), Grismer (1990, 1999b, 2002), Flores Villela (1993), McDiarmid et al. (1999), McPeak (2000), and Nabhan (2003). Wright and Wright (1957), Harris and Simmons (1977, 1978), Campbell and Lamar (1989, 2004), and Grismer (2002) provided maps showing the distribution of the species.

*Crotalus tortugensis* has been included in the following **type lists**: Smith and Taylor (1950) and Slevin and Leviton (1956), **checklists**: Stejneger and Barbour (1923, 1933, 1939, 1943), Smith and Taylor (1945), Loomis et al. (1974), Harding and Welch (1980), Hoge and Romano-Hoge (1981), Murphy (1983c, 2002), Golay et al. (1993), Rubio (1998), and Grismer (1999b), **taxonomic keys**: Cliff (1954a,b), Klauber (1956, 1971, 1972), Wright and Wright (1957), Smith and Taylor (1966), Sanborn and Loomis (1976), De Lisle (1978), and Campbell and Lamar (2004), **scientific and common names lists**: Cuesta Terron (1931), Martín del Campo (1937, 1950), Wright and Wright (1952), Klemmer (1963), Rosenberg (1987), Sokolov (1988), and Liner (1994), and **bibliographies**: Perez Avramow (1969) and Smith and Smith (1976, 1993). Minton et al. (1968) included *Crotalus tortugensis* in a list of venomous snakes occurring in México. Descriptions of habitat were published in Lindsay (1964), McCoy (1984), Mattison (1996), McPeak (2000), and Grismer (2002).

• **ETYMOLOGY.** The name *tortugensis* refers to Tortuga Island, Baja California Sur, México, where the species is endemic.

• **COMMENTS.** *Crotalus tortugensis* is not well differentiated from *C. atrox*. Murphy et al. (2002) and Grismer (2002) main-

tain its status as a separate species, although Murphy et al. (2002) stated that the relationships among the western species of the “*atrox*” group are tenuous. Preliminary ND4 mtDNA sequence data suggest that *C. atrox* is paraphyletic with respect to *C. tortugensis* and all insular forms of *C. atrox* (Castoe, Spencer, and Parkinson, unpublished data).

• **SPECIMENS EXAMINED.** *Crotalus tortugensis*, México: Baja California Sur, Isla Tortuga: CAS 50515 (holotype), 51319, 51320, 51321, 51322, 51323, 51324, 51326, 51327, 51328, 51329, 51330, 51331, 51333, 51334, 51335, 100378, 141792, 204071, 204073, 204074, 204075; CAS-SU 14028; SDSNH 25448, 26798, 26799, 26800, 26801, 26802, 26803, 26804, 26805, 26806, 27077, 27078, 27079, 27080, 27081, 27082.

## LITERATURE CITED

- Altman, P.L. and D.S. Dittmer. 1962. Growth including reproduction and morphological development. Federation of American Societies for Experimental Biology, Washington, D.C.
- Amaral, A. do 1929. Key to the rattlesnakes of the genus *Crotalus* Linne, 1758. Bull. Antivenin Inst. Amer. 3(1):4–6.
- . 1944. Notas sobre a ofiologia neotropical e brasileira. V. Sobre a invalidez específica de *Crotalus unicolor*. Papéis Dep. Zool. S. Paulo 5(5): 29–40.
- Anonymous. 1979. Zu Gast in Reptilienhaus Uhdlingen. Herpetofauna (2):33–34.
- Armstrong, B.L. and J.B. Murphy. 1979. The natural history of Mexican rattlesnakes. Univ. Kansas Mus. Nat. Hist. Spec. Publ. (5):1–88.
- Bowler, J.K. 1977. Longevity of reptiles and amphibians in North American collections. SSAR Herpetol. Circ. (6):1–32.
- Brattstrom, B.H. 1964. Evolution of the pit vipers. Trans. San Diego Soc. Nat. Hist. 13:185–268.
- Brown, J.H. 1973. Toxicology and Pharmacology of Venoms from Poisonous Snakes. Charles C. Thomas, Springfield, Illinois.
- Bücherl, W. and E.E. Buckley. 1971. Venomous Animals and their Venoms. Vol. II. Venomous Vertebrates. Academic Press, New York.
- Campbell, J.A. and W.W. Lamar. 1989. The Venomous Reptiles of Latin America. Comstock Publishing Co., Ithaca, New York.
- and —. 2004. The Venomous Reptiles of the Western Hemisphere. 2 vols. Comstock Publishing Assoc., Cornell Univ. Press, Ithaca, New York.
- Caras, R. 1974. Venomous Animals of the World. Prentice-Hall, Englewood Cliffs, New Jersey.
- Carlquist, S. 1965. Island Life: A Natural History of the Islands of the World. Natural History Press, Garden City, New York.
- Case, T.J. 1978. A general explanation for insular body size trends in terrestrial vertebrates. Ecology 59:1–18.
- . 1983. The reptiles: Ecology. p. 159–209. In T.J. Case and M.L. Cody (eds.), Island Biogeography in the Sea of Cortez. Univ. of California Press, Berkeley, California.
- . 2002. Reptiles: Ecology. p. 221–270. In T.J. Case, M.J. Cody and E. Ezcurra (eds.), A New Island Biogeography of the Sea of Cortés, Oxford Univ. Press, Oxford, England.
- Cliff, F.S. 1954a. Variation and evolution of the reptiles inhabiting the islands in the Gulf of California, Mexico. Unpubl. Ph.D. Diss., Stanford Univ., Stanford, California.
- . 1954b. Snakes of the islands in the Gulf of California, Mexico. Trans. San Diego Soc. Nat. Hist. 12:67–98.
- Cuesta Terron, C. 1931. Los crotalinos mexicanos. An. Inst. Biol. Univ. Mex. 2:47–72.
- De Lisle, H.F. 1978. Key to the snakes of Baja California. Herpetology 9:11–20.
- Ditmars, R.L. 1930. The poisonous serpents of the New World. Bull. New York Zool. Soc. 33:79–132.
- . 1931. Snakes of the World. Macmillan, New York.
- Dowling, H.G. 1951. A proposed standard system of counting ventrals in snakes. British J. Herpetol. 1:97–99.
- Flores Villela, O. 1993. Herpetofauna Mexicana: Annotated list of the species of amphibians and reptiles of Mexico, recent taxonomic changes, and new species. Carnegie Mus. Nat. Hist. Spec. Publ. (17):1–73.
- and P. Gerez Fernández. 1988. Conservación en México: síntesis sobre vertebrados terrestres, vegetación y uso del suelo. Inst. Natl. Invest. Recursos Bioticos, Xalapa, Veracruz, México.
- Gans, C. 1978. Reptilian venoms: Some evolutionary considerations. p. 1–42. In C. Gans and K.A. Gans (eds.), Biology of the Reptilia. Physiology B. Academic Press, New York.
- Glenn, J.L. and R.C. Straight. 1982. The rattlesnakes and their venom yield and lethal toxicity. p. 3–119. In A.T. Tu (ed.), Rattlesnake Venoms: Their Actions and Treatment. Marcel Dekker, New York.
- . 1985. Venom properties of the rattlesnakes (*Crotalus*) inhabiting the Baja California region of Mexico. Toxicon 23:769–775.
- Gloyd, H.K. 1940. The rattlesnakes, genera *Sistrurus* and *Crotalus*: A study in zoogeography and evolution. Chicago Acad. Sci., Spec. Publ. (4):1–270.
- . 1978. The rattlesnakes, genera *Sistrurus* and *Crotalus*: A study in zoogeography and evolution. SSAR Facsimile reprint, Oxford, Ohio.
- Golay, P., H.M. Smith, D.G. Broadley, J.R. Dixon, C. McCarthy, J.G. Rage, B. Schatti, and M. Toriba. 1993. Endoglyphs and Other Major Venomous Snakes of the World. Azemiops S.A., Herpetological Data Center, Aire-Geneva.
- Grismer, L.L. 1990. The reptiles and amphibians of Baja California. Tucson Herpetol. Soc. Newsl. 3:2–6.
- . 1994a. The evolutionary and ecological biogeography of the herpetofauna of Baja California and the Sea of Cortes, Mexico. Unpubl. Ph.D. Diss., Loma Linda Univ., Loma Linda, California.
- . 1994b. Geographical origins for the reptiles on islands in the Gulf of California, Mexico. Herpetol. Nat. Hist. 2(2):17–40.
- . 1999a. An evolutionary classification of reptiles on islands in the Gulf of California, México. Herpetologica 55:446–469.
- . 1999b. Checklist of amphibians and reptiles on islands in the Gulf of California, México. Bull. So. California Acad. Sci. 98:45–56.
- . 2002. The Amphibians and Reptiles of Baja California, its Pacific Islands, and the Islands in the Sea of Cortés, México: Natural History, Distribution and Identification. Univ. California Press, Berkeley.
- Harding, K.A. and K.R.G. Welch. 1980. Venomous Snakes of the World. A Checklist. Pergamon Press, Oxford.
- Harris, H.S., Jr. and R.S. Simmons. 1977. A preliminary account of insular rattlesnake populations, with special reference to those occurring in the Gulf of California and off the Pacific Coast. Bull. Maryland Herpetol. Soc. 13:92–110.
- and —. 1978. A preliminary account of the rattlesnakes with descriptions of four new subspecies. Bull. Maryland Herpetol. Soc. 14:105–211.
- and H.M. Smith. 1979. The current status of names used in Gloyd’s “Rattlesnakes,” p. xvii–xx. In H.K. Gloyd, H.M. Smith, and H.S. Harris, Jr. (eds.), The rattlesnakes, genera *Sistrurus* and *Crotalus*. SSAR Facsimile reprint, Ithaca, New York.
- Hoge, A.R. 1966 (“1965”). Preliminary account on Neotropical Crotalinae [Serpentes: Viperidae]. Mem. Inst. Butantan 32:109–184.
- and S.A.R.W.D.L. Romano. 1971. Neotropical pit vipers, sea snakes, and coral snakes, p. 211–293. In W. Bücherl and E.E. Buckley (eds.), Venomous Animals and their Venoms. Vol. 2: Venomous Vertebrates. Academic Press, New York.
- and —. 1981 (“1978/79”). Poisonous snakes of the world. Part I. Check list of the pit vipers Viperioidea, Viperidae, Crotalinae. Mem. Inst. Butantan (São Paulo) 42/43:179–309.
- Kilmon, J. 1981. The biology of rattlesnakes, p. 26. In J. Kilmon and H. Shelton (eds.), Rattlesnakes in America, Shelton Press, Sweetwater, Texas.
- Kisser, P. 1980. Zur Kenntnis der Klapperschlangen. Herpetofauna (5):6–10.
- Klauber, L.M. 1930. Differential characteristics of southwestern rattlesnakes allied to *Crotalus atrox*. Bull. Zool. Soc. San Diego (6):1–72.
- . 1936a. A statistical study of the rattlesnakes. I. Introduction; II. Sex ratio in rattlesnake populations; III. Birth rate. Occ. Paps. San Diego Soc. Nat. Hist. (1):2–24.
- . 1936b. A key to the rattlesnakes with summary of characteristics. Trans. San Diego Soc. Nat. Hist. 8:185–276.
- . 1937. A statistical study of the rattlesnakes. IV. The growth of the rattlesnake. Occ. Paps. San Diego Soc. Nat. Hist. (3):1–56.
- . 1938. A statistical study of the rattlesnakes. V. Head dimensions. Occ. Paps. San Diego Soc. Nat. Hist. (4):1–53.
- . 1939. A statistical study of the rattlesnakes. VI. Fangs. Occ. Paps. San Diego Soc. Nat. Hist. (5):1–61.
- . 1940. A statistical study of the rattlesnakes. VII. The rattle. Occ.



- Paps. San Diego Soc. Nat. Hist. (6):1–62.
- . 1943. Tail-length differences in snakes, with notes on sexual dimorphism and the coefficient of divergence. *Bull. Zool. Soc. San Diego* (18):3–60.
- . 1956. Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind. 2 Vols. Univ. California Press, Berkeley.
- . 1963. A new insular subspecies of the Speckled Rattlesnake. *Trans. San Diego Soc. Nat. Hist.* 13:73–80.
- . 1971. Classification, distribution, and biology of the venomous snakes of northern Mexico, the United States, and Canada: *Crotalus* and *Sistrurus*, p. 115–156. In W. Bücherl and E.E. Buckley (eds.), *Venomous Animals and their Venoms. Vol. 2: Venomous Vertebrates*. Academic Press, New York.
- . 1972. Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind. 2<sup>nd</sup> ed. 2 Vols. Univ. California Press, Berkeley.
- . 1982. Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind. Abridged ed. Univ. California Press, Berkeley.
- Klemmer, K. 1963. Liste der rezenten Giftschlangen: Elapidae, Hydrophidae, Viperidae und Crotalidae, p. 255–264. In [Die] Giftschlangen der Erde. N.G. Elwert, Marburg.
- Lindsay, G.E. 1962. The Belvedere expedition to the Gulf of California. *Trans. San Diego Soc. Nat. Hist.* 13:1–44.
- . 1964. Sea of Cortez expedition of the California Academy of Sciences. *Proc. California Acad. Sci. Ser. 4*, 30:211–242.
- Liner, E.A. 1994. Scientific and common names for the amphibians and reptiles of Mexico in English and Spanish. *SSAR Herptol. Circ.* (23):1–113.
- Loomis, R.B., S.G. Bennett, S.R. Sanborn, C.H. Barbour, and H. Weiner. 1974. A handlist of the herpetofauna of Baja California and adjacent islands. Priv. Printed. California St. Univ., Long Beach, California.
- Martín del Campo, R. 1935. Nota acerca de la distribución geográfica de los reptiles ponzoñosos en México. *An. Inst. Biol. Univ. México* 6:291–300.
- . 1937. Reptiles ponzoñosos de México. Las víboras de cascabel. *Foll. Divulg. Cient. Inst. Biol. México* (27):1–18.
- . 1950. Serpientes ponzoñosas de México. *Rev. Mex. Cienc. Med. Biol.* 8(53):103–115.
- Mattison, C. 1988. *Keeping and Breeding Snakes*. Blandford Press, London.
- . 1996. *Rattler! A Natural History of Rattlesnakes*. Blandford Press, London.
- Mayr, E. 1942. *Systematics and the Origin of Species from the Viewpoint of a Zoologist*. Columbia Univ. Press, New York.
- McCoy, C.J. 1984. Rattlesnake island. *Notes NOAH* 11:43–44.
- McDiarmid, R.W., J.A. Campbell, and T.A. Touré. 1999. *Snake Species of the World: A Taxonomic and Geographic Reference. Vol. 1. The Herpetologists' League*, Washington, D.C.
- McPeak, R.H. 2000. *Amphibians and Reptiles of Baja California. Sea Challengers*, Monterey, California.
- Minton, S.A., H.G. Dowling, and F.E. Russell. 1968. *Poisonous Snakes of the World. A Manual for Use by U.S. Amphibious Forces*. U.S. Govt. Printing Office, Washington, D.C.
- Murphy, J.B. and B.L. Armstrong. 1978. Maintenance of rattlesnakes in captivity. *Univ. Kansas Mus. Nat. Hist. Spec. Publ.* 3:1–40.
- Murphy, R.W. 1976. The evolution of a peninsular and insular herpetofauna: a drift based alternate hypothesis. Unpubl. M.A. Thesis, San Francisco St. Univ., San Francisco, California.
- . 1982. The genetic relationships and biogeography of the Baja California herpetofauna. Unpubl. Ph.D. Diss., Univ. California, Los Angeles.
- . 1983a. Paleobiogeography and genetic differentiation of the Baja California herpetofauna. *Occ. Pap. California Acad. Sci.* (137):1–48.
- . 1983b. The reptiles: origin and evolution, p. 130–158. In T.J. Case and M.L. Cody (eds.), *Island Biogeography in the Sea of Cortez*. Univ. California Press, Berkeley.
- . 1983c. A distributional checklist of the reptiles and amphibians on the islands in the Sea of Cortez, p. 429–437. In T.J. Case and M.L. Cody (eds.), *Island Biogeography in the Sea of Cortez*. Univ. California Press, Berkeley.
- . 2002. Distributional checklist of nonavian reptiles and amphibians on the islands in the Sea of Cortés, p. 580–585. In T.J. Case, M.J. Cody, and E. Ezcurra (eds.), *A New Island Biogeography of the Sea of Cortés*, Oxford Univ. Press, Oxford.
- and G. Aguirre León. 2002. Nonavian reptiles: Origin and evolution, p. 181–220. In T.J. Case, M.J. Cody, and E. Ezcurra (eds.), *A New Island Biogeography of the Sea of Cortés*, Oxford Univ. Press, Oxford.
- and J.R. Ottley. 1984. Distribution of amphibian and reptiles on islands in the Gulf of California. *Ann. Carnegie Mus.* 53:207–230.
- , D.J. Morafka, and R.D. MacCulloch. 1989. Phylogenetic relationships of rattlesnakes as revealed by protein electrophoresis (abstract). *Texas Herpetol. Soc.*:10.
- , J. Fu, A. Lathrop, J.V. Feltham, and V. Kovac. 2002. Phylogeny of the rattlesnakes (*Crotalus* and *Sistrurus*) inferred from sequences of five mitochondrial DNA genes, p. 69–92. In G.W. Schuett, M. Höggren, M.E. Douglas, and H.W. Greene (eds.), *Biology of the Vipers*. Eagle Mountain Publishing, LC, Eagle Mountain, Utah.
- Nabhan, G.P. 2003. *Singing the Turtles to Sea: The Comcáac (Seri) Art and Science of Reptiles*. Univ. California Press, Berkeley.
- Pérez Avramow, R. 1969. Bibliografía comentada relativa a las víboras de cascabel mexicanas del género *Crotalus*. *Biol. Diss., Univ. Natl. Aut. México, México*.
- Perkins, C.B. 1948. Longevity of snakes in captivity in the United States. *Copeia* 1948:217.
- . 1950. Longevity of snakes in captivity in the United States. *Copeia* 1950:238.
- . 1951. Longevity of snakes in captivity in the United States. *Copeia* 1951:182.
- . 1952. Longevity of snakes in captivity in the United States. *Copeia* 1952:280–281.
- . 1953. Longevity of snakes in captivity in the United States as of January 1, 1953. *Copeia* 1953:243.
- . 1954. Longevity of snakes in captivity in the United States as of January 1, 1954. *Copeia* 1954:229–230.
- . 1955. Longevity of snakes in captivity in the United States as of January 1, 1955. *Copeia* 1955:262.
- Phelps, T. 1984. *Poisonous Snakes*. Blandford Press, Dorset, England.
- Radcliffe, W.C. and T.P. Maslin. 1975. A new subspecies of the Red Rattlesnake, *Crotalus ruber*, from San Lorenzo Sur Island, Baja California Norte, Mexico. *Copeia* 1975:490–493.
- Rego, A.A. 1980/1981. Sobre a identificação das espécies de *Porocephalus* (Pentastomida) que ocorrem em ofídios da América tropical. *Mem. Inst. Butantan* 44/45:219–231.
- Riley, J. and J.T. Self. 1979. On the systematics of the pentastomid genus *Porocephalus* (Humboldt, 1811) with descriptions of two new species. *Syst. Parasitol.* 1:25–42.
- Rosenberg, P. 1987. Common name index: poisonous animals, plants and bacteria. *Toxicon* 25:799–890.
- Rubio, M. 1998. *Rattlesnake: Portrait of a Predator*. Smithsonian Institution Press, Washington, D.C.
- Russell, F.E. 1969. Crotalidae of the Western Hemisphere. *Herpeton* 4:1–8.
- . 1979. The clinical problem of crotalid snake venom poisoning, p. 978–996. In C.-Y. Lee (ed.), *Snake Venoms, Handbook of Experimental Pharmacology*, Springer-Verlag, Berlin.
- . 1980. *Snake Venom Poisoning*. Lippincott, Philadelphia.
- . 1983. *Snake Venom Poisoning*. Scholium Intl., Inc., New York.
- Ruth, S.B. 1974. A kingsnake from Isla Tortuga in the Gulf of California, Mexico. *Herpetologica* 30:97–98.
- Sanborn, S.R. and R.B. Loomis. 1976. *Keys to the amphibians and reptiles of Baja California, Mexico, and the adjacent islands*. Priv. printed, California St. Univ., Long Beach.
- Savage, J.M. 1952. A preliminary checklist to the herpetofaunas of the islands adjacent to Baja California, Mexico. Unpubl. ms.
- Schmidt, K.P. 1922. The amphibians and reptiles of Lower California and the neighboring islands. *Bull. Amer. Mus. Nat. Hist.* 46(Art. 11): 607–707.
- Shaw, C.E. 1957. Longevity of snakes in captivity in the United States as of January 1, 1957. *Copeia* 1957:310.
- Skoczylas, R. 1978. Physiology of the digestive tract, p. 589–717. In C. Gans and K. Gans (eds.), *Biology of the Reptilia. Vol. 8. Physiology*. B. Academic Press, New York.
- Slavens, F.L. 1978–2000. *Reptiles and Amphibians in Captivity: Breeding, Longevity and Inventory*. Priv. printed, Seattle.
- Slevin, J.R. and A.E. Leviton. 1956. Holotype specimens of reptiles and amphibians in the collection of the California Academy of Sciences. *Proc. California Acad. Sci.* 28:529–560.
- Smith, H.M. and R.B. Smith. 1976. *Synopsis of the Herpetofauna of Mexico. Vol. III. Source Analysis and Index for Mexican Reptiles*.

- John Johnson, North Bennington, Vermont.
- and —. 1993. Synopsis of the Herpetofauna of Mexico. Vol. VII. Bibliographic Addendum IV and Index, Bibliographic Addendum II–IV 1979–1991. Univ. Press Colorado, Niwot.
- and E.H. Taylor. 1945. An annotated checklist and key to the snakes of Mexico. *Bull. U.S. Natl. Mus.* (187):1–239.
- and —. 1950. Type localities of Mexican reptiles and amphibians. *Univ. Kansas Sci. Bull.* 33:313–380.
- and —. 1966. Herpetology of Mexico. Annotated Checklists and Keys to the Amphibians and Reptiles. (A Reprint of Bulletins 187, 194, and 199 of the U.S. Natl. Mus., with a list of subsequent taxonomic innovations). Eric Lundberg, Ashton, Maryland.
- Snider, A.T. and J.K. Bowler. 1992. Longevity of reptiles and amphibians in North American collections. 2<sup>nd</sup> ed. *SSAR Herpetol. Circ.* (21):1–40.
- Sokolov, V.E. 1988. Dictionary of Animal Names in Five Languages. Amphibians and reptiles. Russky Yazyk, Moscow.
- Soulé, M.E. and A.J. Sloan. 1966. Biogeography and distribution of reptiles and amphibians on islands in the Gulf of California, Mexico. *Trans. San Diego Soc. Nat. Hist.* 14:137–156.
- Spencer, C.L. 2003. Geographic variation in the morphology, diet and reproduction of a widespread pitviper, the Western Diamondback Rattlesnake (*Crotalus atrox*). Unpubl. Ph.D. Diss., Univ. Texas, Arlington.
- Stejneger, L. and T. Barbour. 1923. A checklist of North American Amphibians and Reptiles. 2<sup>nd</sup> ed. Harvard Univ. Press, Cambridge, Massachusetts.
- and —. 1933. A checklist of North American Amphibians and Reptiles. 3<sup>rd</sup> ed. Harvard Univ. Press, Cambridge, Massachusetts.
- and —. 1939. A checklist of North American Amphibians and Reptiles. 4<sup>th</sup> ed. Harvard Univ. Press, Cambridge, Massachusetts.
- and —. 1943. A checklist of North American Amphibians and Reptiles. 5<sup>th</sup> ed. Harvard Univ. Press, Cambridge, Massachusetts.
- Stewart, S.G. and D.J. Morafka. 1989. Karyotypes of Gulf of California insular rattlesnakes (Viperidae: *Crotalus*) compared to those of peninsular sister taxa (abstract). First World Congress of Herpetology, Canterbury, England.
- , —, and A.D. Stock. 1990. Karyotypes of Gulf of California insular rattlesnakes (Viperidae: *Crotalus*) compared to those of peninsular sister taxa, p. 261–266. *In* E. Olmo (ed.), *Advances in Life Sciences, Cytogenetics in Amphibians and Reptiles*, Birkhauser, Basel.
- Stille, B. 1987. Dorsal scale microdermatoglyphics and rattlesnake (*Crotalus* and *Sistrurus*) phylogeny (Reptilia: Viperidae: Crotalinae). *Herpetologica* 43:98–104.
- Tryon, B.W. 1986. The island, the rattlesnake, and the species survival plan. *Bull. British Herpetol. Soc.* (16):20–24.
- Underwood, G.L. 1979. Classification and distribution of venomous snakes of the world, p. 15–40. *In* C.-Y. Lee (ed.), *Snake Venoms: Handbook of Experimental Pharmacology*, Springer-Verlag, Berlin.
- Van Denburgh, J. 1922. The reptiles of western North America. Vol. II: Snakes and turtles. *Occ. Pap. California Acad. Sci.* (10):617–1028.
- and J.R. Slevin. 1921. Preliminary diagnoses of more new species of reptiles from islands in the Gulf of California, Mexico. *Proc. California Acad. Sci. Ser. 4*, 111(117):395–439.
- Werner, F. 1923. Uebersicht der Gattungen und Arten der Schlangen der Familie Colubridae. I. Teil mit einem Nachtrag zu den übrigen Familien. *Arch. Naturgesch.* 89:138–199.
- Wright, A.H. and A.A. Wright. 1952. List of the snakes of the United States and Canada by states and provinces. *Amer. Midl. Nat.* 48:574–603.
- and —. 1957. *Handbook of Snakes of the United States and Canada*. 2 Vols. Comstock Publ. Assoc., Ithaca, New York.

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